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On the hypothesis of dioicous − monoicous species pairs in the Mniaceae (Bryophyta); morphology, sexual condition and distiribution

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On the hypothesis of dioicous − monoicous species pairs in the Mniaceae (Bryophyta); morphology, sexual condition and distiribution. – Acta Mus. Siles. Sci. Natur., 68: 67-81, 2019.

Abstract: Some early observations seemed to show that, in the Mniaceae, the doubling of the chromosome set affects a change from dioicous to monoicous condition, larger size of the gametophyte including larger leaf cell size, and to a wider range of the monoicous counterpart. The Mniaceae taxa are divided into four groups based on their sexual condition and morphology. 1. Dioicous – monoicous counterparts which can be distinguished by morphological characters, 2. Dioicous – monoicous taxa which have no morphological, deviating characters, 3. Monoicous species mostly with diploid chromosome number for which no dioicous counterpart is known, and 4. The taxa in Mniaceae with only dioicous plants. Most of the monoicous species of the Mniaceae have wide ranges, but a few of them are endemics in geographically isolated areas. The dioicous species have either a wide holarctic range or a limited range in the forested areas of temperate and meridional North America, Europe and SE Asia, or in subtropical Asia. Some of the monoicous species are evidently autodiploids and a few of them are allopolyploids from cross-sections of two species. Quite recently, several new possible dioicous – monoicous relationships have been discovered.

Key words: allopolyploids, autopolyploids, *Cinclidium*, *Cyrtomnium*, characters, diploids, floristic elements, haploids, *Leucolepis*, *Mnium*, new combination, *Orthomnion*, phytogeography, *Plagiomnium*, *Pseudobryum*, *Rhizomnium*, taxonomy, *Trachycystis*, number of species, polyploids, ranges

Introduction

The dioicous − monoicous species pairs in the Mniaceae were discovered by Lowry (1948). He proposed four monoicous – dioicous pairs (see below). The idea was that the doubling of the chromosome set causes a monoicous condition of the plant, a larger size and larger leaf cells. Wettstein's (1924, 1938, 1942, Wettstein & Staub 1942) experiments gave some grounds to this hypothesis. He had produced experimentally diploid *Funaria hygrometrica* Hedw. and diploid new taxon, *Bryum correnssii* Wettst. The diploid plants showed gigantism in both the cell size and the plant body as a whole. Koponen (1967, 1971a, 1973a), Bowers (1969a,b, 1980), Mogensen (1973) and Koponen and Nilsson (1978) discussed on the topic and proposed changes and additions to Lowry's concept.

Koponen (1981a) examined Lowry's voucher specimens and found that many of them were not correctly identified. Wyatt (1985) confirmed Koponen's identifications and reviewed the earlier studies on the topic. Later R. Wyatt, in many papers (Wyatt *et al*. 1988, 1992, 1993a, b, 2013, Wyatt & Odrzykoski 1989, 2012), returned to the topic and showed that although some of the species pairs seem to be autopolyploids, some of them actually are allopolyploids caused by cross-sections between species.

The moss family Mniaceae, in the sense of Koponen (1968a, 2017, Koponen & Sun 2017), has 74 species + *Ciclidium minutifolium* (Koponen & Ignatova 2018) worldwide. In this paper, I summarize the studies of the dioicous – monoicous species pairs of the Mniaceae and try to evaluate the morphological characters and phytogeography useful in separating these pairs of taxa. The world ranges of taxa and floristic elements are reviewed in relation to their monoicous or dioicous sexuality.

The chromosome numbers in the lists below are from Bowers (1980) and Fritsch (1982), and later counts from "Index to plant chromosome numbers" 1972−2006. The count for *Plagiomnium floridanum* is according to Wyatt & Odrzykoski (2012). The world ranges are from Koponen (2017). The author abbreviations are given on the lists below.

Lowry's (1948) dioicous – monoicous species pairs

The dioicous − monoicous species pairs within the traditional Mniaceae recognized by Lowry (1948) were:

	n ♂♀		**2n**, monoicous
Mnium affine Funck	6	*M. medium* Bruch & Schimp.	12
M. cuspidatum Hedw.	6	*M. cuspidatum* Hedw.	12
M. punctatum Hedw.	7	*M. pseudopunctatum* Bruch & Schimp.	14
M. orthorrhynchum auct. (= *M. thomsonii* Mitt.)	6	*M. marginatum* (Dicks.) P. Beauv.	12

However, the species pairs Lowry proposed do not hold, since his material was partly misidentified (Koponen 1981a, Wyatt 1985). Also, the morphological characters such as laminal cell size or shape do not fit in all pairs.

According to the prevailing North American tradition, Lowry (1947) named his first dioicous counterpart as *Mnium affine* (*Plagiomium a*.). The voucher specimens were identified as *Plagiomnium ellipticum* (Koponen 1981a). *P. ellipticum* is not a convenient counterpart of *P. medium*. *P. ellipticum* has wider bipolar range than *P. medium*, which is rather strictly delimited to boreal zone of the northern hemisphere (Koponen 1971a, 2014a). The shape of laminal leaf cells and teeth of leaf border are different. A character of *P. ellipticum*, which hardly has connection with the number of chromosomes, is the non-decurrent leaves. All the other species of *Plagiomium* section *Rosulata* have decurrent leaf bases (Koponen 1971a). Only two other species of *Plagiomnium*, *P. rostratum* and *P. succulentum* in the section *Rostrata*, have non-decurrent leaves. The loss of decurrency of leaf bases must be a result of a long-lasting evolutionary history.

Lowry (1948) discovered that in American *Mnium cuspidatum* (*Plagiomnium c*.) the chromosome numbers 6 and 12 occur. This was confirmed by Wyatt & Odrzykoski (2012, see below under *P. floridanum*).

Lowry's (1948) dioicous – monoicous pair *Mnium punctatum* (*Rhizomnium p*.) and *Mnium pseudopunctatum* (*Rhizomnium p*.) have differences in many characters, which hardly can be caused by the doubling of the chromosomes. They have different rhizoid topography. *R. punctatum* has only axillary macronemata while both macronemata and micronemata are present in *R. pseudopunctatum* (Koponen 1968b, 1971b, 1973a, 2014b). The capsules differ, *R. pseudopunctatum* has a ± globose, brownish capsule and brown peristome with less than 20 lamellae of the outer peristome teeth, while the capsule of *R. punctatum* is elongate, yellowish or pale and the number of lamellae is more than 20 (Koponen 1968b, 2014b). The analyses based on DNA characters (Koponen & Sun 2017) showed that *Rhizomnium horikawae*, which is closely related to *R. punctatum*, is distant from *R. pseudopunctatum*. Koponen & Sun (2017) placed them in different sections of *Rhizomnium*, *R. punctatum* in the section *Rhizomium*, and *R. pseudopunctatun* in the section *Macromnium*.

Mnium orthorrhynchum auct. (= *M. thomsonii* Mitt.) and *M. marginatum* could be a species pair, as Lowry proposed. The leaf cells in *M. thomsonii* are smaller than the cells of *M. marginatum*, and both are calcicole species. However, the shape of laminal cells and the leaf areolation as a whole are different. *M. thomsonii* has ± quadrate or isodiametric laminal cells with firm cell walls and the cell size is uniform, best observed by comparing the laminal cells near the costa and at the leaf border. In *M. marginatum* the laminal cells near the costa are

distinctly larger than the cells at leaf border, shortly elongated to rhomboidal and ± thick-walled with distinct trigones. The teeth of the dorsal costa are numerous in *M. thomsonii* and the leaf marginal teeth are sharp, while the teeth of costa are few or absent in *M. marginatum*, and its leaf marginal teeth are smaller and blunt. *M. lycopodioides* could more probably be the dioicous counterpart of *M. marginatum*, but see below under *Mnium marginatum*.

Concluding: The dioicous – monoicous species pairs proposed by Lowry (1948) do not fulfill the morphological nor phytogeographical requirements of dioicous – monoicous species pairs in the Mniaceae, except the pair *Plagiomnium cuspidatum* (n = 6) − *P. cuspidatum* (n = 12).

Sexual condition and morphology in the species of the Mniaceae

On the basis of morphology, the dioicous – monoicous taxa in the Mniaceae can be divided into two groups:

1. Morphologically differing pairs
2. Morphologically similar monoicous and dioicous taxa

However, the majority of taxa in the Mniaceae do not show the dioicous – monoicous partnership:

3. Species of which only monoicous plants are known
4. Species of which only dioicous plants are known

Morphologically differing monoicous – dioicous species pairs

	n ♂♀		**2n**, monoicous
Cinclium arcticum (Bruch & Schimp.) Schimp.	7	*C. stygium* Sw.	14
C. minutifolium Broth.	-	*C. subrotundum* Lindb.	14
Plagiomnium floridanum R. Wyatt & Odrzykoski	6	*P. cuspidatum* (Hedw.) T.J. Kop.	12
P. insigne (Mitt.) T.J. Kop.	7	*P. medium* (Bruch. & Schimp.) T.J. Kop.	12
(or *P. ellipticum* × *P. insigne*)		*P. medium*	12
P. maximoviczii (Müll. Hal.) T.J. Kop.	6, 7	*P. rhynchophorum* (Hook) T.J. Kop.	12
Rhizomnium gracile T.J. Kop.	7	*R. pseudopunctatum* (Bruch & Schimp.) T.J. Kop.	13, 14

These dioicous – monoicous species pairs can be separated from each other not only by the sexual condition but also by morphologic characters. In most cases synoicous plants are stronger and taller and their laminal cells are larger than in their dioicous counterparts. Most of the synoicous plants have wider ranges than their haploid and dioicous pairs, and the ranges are partly sympatric. The specific status has been generally accepted to these sister species. Some additions to their taxonomy and ranges are made here.

Cinclium arcticum – C. stygium

Mogensen (1973) studied the morphology and phytogeography of the species of *Cinclidium* and came to the conclusion that *Cinclium arcticum – C. stygium* are a species pair. They fulfil the morphological and geographical prerequisites of species pairs. *C. arcticum* is smaller in size and its leaf cells are also smaller. It is a circumpolar, high arctic – oroarctic species of the northern hemisphere while *C. stygium* has a wide-ranging circumpolar distribution in the boreal to arctic regions of the northern hemisphere and is bipolar (Mogensen (1973). Both of them grow in moist to wet habitats such as bogs and marshes, but *C. arcticum* is more restricted to calcareous or eutrophic subsoil. According to Wyatt *et al*. (2013) *C. stygium* may be an allopolyploid origin from *C. arcticum* and *C. latifolium*, but it is also possible that *C. stygium* is an autopolyploid, most likely of *C. arcticum*. Pineiro *et al*. (2012) did not rule out this possibility.

Cinclidium minutifolium – C. subrotundum

Koponen and Ignatova (1918) accepted *Cinclidium minutifolium* Broth., which on the basis on the elongated macronematous rhizoid apparatus is a species of *Cinclidium* (Koponen & Ignatova 2018, fig. 247 E). It has similar orbicular leaf shape as *C. subrotundum*, but has unistratose leaf border against bistratose in *C. subrotundum*. The dioicous sexual condition and smaller leaf cells than in *C. subrotundum* and smaller but partly sympatric range fulfill the prerequisites of species pair relationship. According to Mogensen (1973) and Koponen and Ignatova (2018), *Cinclidium subrotundum* has a circumpolar holarctic range and *C. minutifolium* occurs in arctic Asia and northern European Russia (Koponen & Ignatova 2018). However, the relationship of these taxa still needs genetic and sequence confirmation. It may be mentioned that Wyatt *et al*. (2013) discovered an unknown "*Cinclidium* species A" from Alaska, different from other four species accepted e.g. by Mogensen (1973). Also, Pineiro *et al*. (2013) discovered an unknown *Cinclidium*, which according to M. Ignatov (pers. comm.) agrees with *C. minutifolium*.

Plagiomnium floridanum – P. cuspidatum

Bowers (1969a) proposed that *Mnium cuspidatum* (= *Plagiomnium c*.) and *M. trichomanes* Mitt. (= *Plagomnium acutum*) seem to be a natural species pair. *Plagiomnium acutum* has smaller laminal cell size (Koponen 1981b, diagram in fig. 20). Also, the leaf and cell sizes of many voucher specimens of chromosome counts of *P. acutum* (n = 6) and *P. cuspidatum* (n = 12) differ clearly (Koponen 1981b, diagram in fig. 21). The study includes *Schornherst* specimen from Florida, for which Lowry (1948) published the chromosome count n = 6. In the diagram, the *Schonherst* specimen differs distinctly from *P. acutum* and less clearly from *P. cuspidatum*. The range of *P. acutum* is limited to SW Asia (Koponen 1981b, 2014a, c) and, accordingly, smaller than the range of circumpolar, holarctic *P. cuspidatum*. However, the phylogenetic study by Koponen & Sun (2017) proposed that instead of *P. cuspidatum*, the specific pair counterpart of *P. cuspidatum* is *P. floridanum*, as was already assumed by Wyatt and Odrzykoski (1998, 2012). *P. floridanum* has a limited range in North America in Florida, Georgia and Mississippi. *P. floridanum* is a calcicole, and it can be hypothetized that the change to more acid substrates, together with secured fertilization, favored the new diploid *P. cuspidatum* to spread to new territories.

Plagiomnium insigne – P. medium

This pair fulfils the characters of a dioicous – monoicous species pair (Koponen 1967, 1971a). The chromosome set is double in *P. medium*, its laminal cells are larger, and *P. medium* has a circumpolar holarctic range, while *P. insigne* is an endemic of western North America (Koponen 1971a). Their laminal cell shape is ± isodiametric and with distinct trigones. Leaf marginal teeth are similar, large, sharp and formed by one or two cells and projecting towards the leaf apex. In the other dioicous species of *Plagiomnim* section *Rosulata* the leaf cells are elongated with ± firm walls, and their leaf marginal teeth, except *P. ellipticum*, are formed by (1)2–4 cells projecting to different directions (Koponen 1971a, Jia & He 2014). The substrates of *P. insigne* and *P. medium* are similar (Koponen 1971a).

However, Wyatt *et al*. (1988, 1992) presented that the electrophoretic patterns witness that *Plagiomnium medium* is an allopolyploid originating from the cross-section between *Plagiomnum ellipticum* × *P. insigne.* According to Koponen (1971a: 360), *P. insigne, P. medium* and *P. rugicum* (Brid.) T.J. Kop. (= *P. ellipticum*) are united by the acute leaf apex, teeth of leaf margin with 1 or 2 sharp cells, and laminal cells which are near to being isodiametric, although in the last respect *P. ellipticum* deviates from the other two species. *P. ellipticum* differs from *P. insigne* and *P. medium* clearly, e.g. having shorter and smaller teeth of leaf margin than any

other taxon of the section (except *P. medium* ssp. *curvatulum*) and especially in the absence of decurrent leaf bases. Accordingly, when observed from the morphological point of view, the possible allopolyploid *P. medium* has inherited more characters from *P. insigne* than from *P. ellipticum*. Also, the wide ecological amplitude of *P. ellipticum* in many kinds of wet to moist, acid to eutrophic habitats and substrates changed to more uniform habitats on moist to mesic forest soils. The ranges of *P. insigne* and *P. ellipticum* are not sympatric, but may have been, since *P. ellipticum* is bipolar occurring in S Chile and S Argentina.

McIntosh and Newmaster (2014a) reported one collection of *Plagiomnium medium* from British Columbia, which is dioicous and has larger leaves and laminal cells than the other populations of *P. medium*, suggesting that it could possibly be an undescribed species. I have seen one similar specimen (male plants) collected in South Finland. Since these two finds were from widely distant localities, they may simply represent an accidental phenomenon not worth taxonomic recognition. A similar case is dioicous *Mnium arizonicum* (n = 6) and *M. saximontanum* (n = 12), which, in spite of the double chromosome number, is dioicous (Bowers 1969b). Koponen (1974a) synonymized these taxa and *M. saximontanum* was not mentioned by McIntosh and Newmaster (2014b).

Plagiomnium maximoviczii – P. rhynchophorum

Synoicous *Plagiomnum rhynchophorum* has larger laminal leaf cells than dioicous *P. maximovizii*. They fulfil the prerequisite of a díoicous – synoicous pair as to their distribution areas. *P. maximoviczii* has SE Asiatic range while *P. rhynchphorum* is pansubtropical and present in SE Asia, Africa and South America, with disjunct occurrences in southern Appalachians and Hawai'i in U.S.A (Koponen 1972a, 1979, 1981c, 1982c). They grow in forest sites on various substrates (Koponen 1972a, 1974b, 2014c).

In *Plagiomnium* section *Rostrata,* the three synoicous species are *Plagiomnim rostratum, P. rhynchophorum* and *P. novae-zealandiae*, and dioicous species number six (Koponen 1972a, 1982a). Koponen (1982a) hypothetized on the phylogeny of the species in the section *Rostrata*, and concluded that *P. maximoviczii* and *P. rhynchophorum* are close relatives by having similar distinct juxtacostal cells and long teeth of leaf margin formed by (1)2–4 cells (at least in well-developed fertile plants). Moreover, they both have long-decurrent leaves. The leaves in *P. rostratum* are non-decurrent (populations with short leaf decurrences occur in the Baikal area in Siberia) and the teeth of leaf margin are smaller and formed by one blunt cell. In the phylogenetic analysis by Koponen and Sun (2017) *P. maximoviczii* and *P. rhynchophorum* form a pair distant from the other taxa (*P. integrum, P. succulentum*) of the section *Rostrata*, which were included in their study. Harris (2008) could not present any clear-cut solution on the relationships of the taxa in the section *Rostrata*. In two of his cladograms *P. maximoviczii* is a sister species of *P. rostratum* and *P. novae-zealandiae*, but at the same time *P. maximoviczii* and *P. rhynchophorum* are in the same glade with *P. integrum* and *P. vesicatum*. As to *P. novae-zealandiae*, see below.

Rhizomnium gracile − R. pseudopunctatum

Dioicous *Rhizomnium gracile* and monoicous *R. pseudopunctatum* fullfil the prerequisities of a dioicous – monicous species pair. *R. gracile* is smaller and has a boreal, N. American range extending to easternmost Asia (Koponen & Afonina 1992, Koponen & Ignatova 2018), with a single locality in Europe (Koponen 2015). *R. pseudopuncatum* has much wider arctic to boreal continuously holarctic range. Also, they both grow in ± eutrophic swamp and fen habitats on wet peat or muddy soil. Both of them have a globose capsule and the peristomes are similar: brown and less than 20 lamellae on the outer peristome teeth. This separates them from all other species of *Rhizomnium*, which have elongated, pale capsule and exothecial teeth are yellow and have more than 20 lamellae (Koponen 1968b, 1973a, 2014b). Bowers (1969a) thought that

Mnium andrewsianum (*Rhizomnium a*.) and M. *pseudopunctatum* (*Rhizomnium p*.) form a species pair. He was actually correct, since *R. gracile* was separated only later by Koponen (1973a) from *R. andrewsianum*.

According to Wyatt *et al*. (1993a) the isozyme evidence proves that the moss *Rhizomnium pseudopunctum* is an allopolyploid of *R. gracile x R. magnifolium*, and Jankowiak *et al*. (2005) found additional evidence of the allopolyploidy of *R. pseudopunctatum*. The existence of both monoicous and dioicous races of *R. magnifolium* (see below) perhaps makes the situation more complicated. In the cladogram by Koponen and Sun (2017), monoicous *R. magnifolium* and *R. pseudopunctatum* are sister species, and both are sisters to synoicous race of *R. magnifolium*. In any case, *R. pseudopunctatum* has inherited the orbicular leaf shape and the sporophyte from *R. gracile*, not from *R. magnifolium*. See also below under *Rhizomnium magnifolium*.

Morphologically similar dioicous and monoicous taxa

The second group is composed of several taxa including both dioicous and synoicous plants, which I have not been able to distinguish morphologically from each other. The chromosome numbers of most these taxa are not known.

The fact that all of these dioicous – monoicous taxa occur in the SE Asia may suggest that the evolution of the mniaceous taxa is still rapidly ongoing in that area. Another point worth noting is that new taxa have been described quite recently from there: *Orthomnion piliferum* and *O. noguchii* (Koponen 1980a), *Orthomnion yunnanense* (Koponen, Li & Zang 1982), *Plagiomium cordatum* (Koponen & Norris 1983), *Mnium orientale* (Wyatt *et al*. 1997), *Orthomnion wui* (Koponen 2007) and *Plagiomnium quizhouense* (Jia & He 2014). Moreover, Harris (2008) discovered two possibly new undescribed taxa based on chloroplast phylogenies in *Plagiomnium*.

	n ♂♀		**2n**, monoicous
Orthomnion dilatatum (Mitt.) P.C. Chen	-	*O. dilatatum*	12
O. yunnanense T.J. Kop., X.J. Li & M. Zang	-	*O. wui* T.J. Kop.	-
Plagiomnium succulentum (Mitt.) T.J. Kop.	7	*P. succulentum*	-
Rhizomnium magnifolium (Horik.) T.J. Kop.	7	*R. magnifolium*	-

Orthomnion dilatatum ♂♀ − *Orthomnion dilatatum*, monoicous

The populations of *Orthomnion dilatatum* occurring in Japan, Taiwan and the Philippines are synoicous while the dioicous plants occur in western SE Asia (Koponen 1980a). However, a synoicous specimen was recently reported from India (Koponen 2014c).

Orthomnion yunnanense ♂♀ − *O. wui*, monoicous

One of the most recently discovered example of this group seems to be the "pair" comprising the dioicous *Orthomnion yunnanense* and the synoicous *O. wui*. They cannot be separated morphologically. The taxonomy of the latter was studied by Jia and He (2015) and they transferred *O. wui* to *Plagiomnium*, with good reasons (see Chapter 4).

Plagiomnium. succulentum ♂♀ − *P. succulentum*, monoicous

Koponen & Norris (1983) discovered that the plants of *Plagiomnium succulentum* in New Guinea are synoicous, while in the other part of the range they are dioicous (e.g. Noguchi 1989). However, synoicous plants occur in the Himalayan area as well (NW Himalaya, Mussoorie, 5500', 25.10.1897 *P.W. Mackinnon* (H-BR 2806003, as *Mnium Mackinnonii* Broth. (ex Kabiersch *nom. nud.*, 1936).

Rhizomnium magnifolium ♂♀ − *R. magnifolium*, monoicous

The synoicous plants of *Rhizomnium magnifolium* (as *R. perssonii* T.J. Kop.) were first identified from Taiwan (Koponen 1971c) and when material with sporophytes could be studied from the Himalayan area (Koponen 2014b) the morphological identity of dioicous and monoicous plants was obvious. The synoicous race of *Rhizomnium magnifolium* ranges from Taiwan to the Himalayas (Koponen 2014b), while the dioicous race is a holarctic circumpolar taxon (Koponen 1968b, 1971c, 1973a, Koponen & Afonina 1992, Koponen & Ignatova 2018). Both dioicous and synoicous specimens were included in the analysis by Koponen & Sun (2017) and showed close relationship.

Species with only monoicous plants

	2n	**range**
Mnium marginatum (Dicks.) P. Beauv.	12	circumpolar holarctic
M. spinulosum Bruch & Schimp.	8	circumpolar holarctic
Plagiomnium curvatulum (Lindb.) Schljakov	12	circumpolar holarctic
P. drummondii (Bruch & Schimp.) T.J. Kop.	6	circumpolar holarctic
P. novaezealandiae (Col.) T.J. Kop.	14	Australia, New Zealand
P. rostratum (Schrad.) T.J. Kop.	12	disjunctively holarctic
P. venustum (Mitt.) T.J. Kop.	12	Pacific N America

This group is formed by synoicous species, which have no morphologically similar dioicous counterpart. The explanation for this could be that the doubling of chromosomes resulting in synoicy confirmed the fertilization and the continuous production of spores. The new synoicous plant had the opportunity to spread to different areas and substrates and to adapt to climatic changes. The dioicous ancestor did not have this possibility and became extinct. The wide ranges of *Mnium marginatum, M. spinulosum, M. drummondii* and *Plagiomnium rostratum* concur with this hypothesis. *P. venustum* and *P. novae-zealandiae* remained geographically isolated. Of *P. curvatulum*, see below.

Mnium marginatum

Bowers (1969) proposed that *Mnium ambiguum* H. Müll. (= *M. lycopodioides*) and *Mnium marginatum* form a species pair. They seem to fulfil the prerequisite of a dioicous – monoicous species pair, *M. lycopodioides* has smaller leaf cells than *M. marginatum*. However, the shape of leaf cells is not quite identical. *M. lycopodioides* in general has ± isodiametric to slightly elongated, thin-walled laminal cells with distinct trigones, while the cells in *M. marginatum* tend to be relatively longer with thicker walls, best seen in the cells close to the costa. The characters not fulfilling the demands of species pairs are the teeth of leaf margin and costa: *M. lycopodioides* has sharp teeth while the teeth of leaf margin in *M. marginatum* are blunt and the costa is smooth or there are a few blunt teeth. This does not fit to the theory of dioicous – monoicous species pairs; compared with *Plagiomium insigne – P. medium* and *P. floridanum – P. cuspidatum* in which the teeth characters are similar. One character present in many populations of *M. marginatum* is the long cuspidate leaf apex, which is gradually acute in *M. lycopodioides*. Also, the ranges of these two taxa do not support their species pair connection. Both of them are holartic, but the range of *M. marginatum* is more limited. It has ± continuous range in North America and Europe but in Asia it is rare in China and absent from Japan. *M. lycopodioides* has wider range in North America (Koponen 1979, map as *M. ambiguum*), North Asia (Koponen & Ignatova 2018) and SE Asia (Koponen 2014c,) than the range of *M. marginatum.* On the contrary, in Scandinavia (Söderström *et al*. 1998) and Britain (Blockeel *et al*. 2014), and obviously in other parts of Europe *M. lycopodioides* is rare (Frey *et al*. 1995), occurring only in boreal and oroboreal areas, while *M. marginatum* is temperate.

However, *M. lycopodioides* is heterogeneous in some characters such as the size and the number of the teeth on the costa. In western North America large-sized plants, known as *M. umbratile* Mitt. occur, while in SW Asia plants of some of populations are much smaller (*M. laevinerve* Cardot). In Japanese populations the number of teeth on the costa varies, and plants with a smooth costa exist (Koponen 2014c). *M. lycopodioides* grows in many mesic substrates (Koponen 2014c) while *M. marginatum* is a calcicole. A similar difference is absent in the pairs *Plagiomium insigne – P. medium* and *P. maximoviczii – P. rhynchophorum.*

In this connection it may be relevant to remind that a dioicous population of *Mnium marginatum*, named as *M. riparium* Mitt., has once been found in Britain (Koponen 1980b).

Mnium spinulosum

Mnium spinulosum has the chromosome number 8, differing of that of other species of *Mnium*. It has a strong leaf border, and teeth of leaf margin and costa are similar to those in *M. spinosum*. The laminal cell characters do not support their dioicous – monoicous species pair relationship, neither the chromosome number of *M. spinosum* which is 6. The laminal cells in *M. spinulosum* are ± isodiametric and not in rows. The leaf cells in *M. spinosum* are elongated and arranged in diagonal rows from costa to border. *M. spinulosum* has wider holarctic mainly boreal range, while *M. spinosum* is more northern extending from boreal to oroarctic zones in Eurasia. It is absent from western North America (Koponen 1973b, Steere 1974).

Plagiomnium curvatulum

Wyatt *et al*. (1993b) postulated, with good grounds, that *Plagiomnium curvatulum* most probably is an allopolyploid of two dioicous taxa, *P. ellipticum* (n = 6) and *P. elatum* (n = 6), or of the ancestor of the latter, *P. "semielatum"*. Koponen (1971a) discussed at length on the characters of *P. curvatulum* (as *P. medium* ssp. *curvatulum* (Lindb.) T.J. Kop.) comparing it mainly to *P. medium* ssp. *medium*. He also mentioned the difficulty to distinguish especially the sterile shoots of *P. curvatulum* from *P. ellipticum*. The characters which *P. curvatulum* evidently inherited from *P. ellipticum* are dominant in the morphology of *P. curvatulum.* These include the small-sized teeth of the leaf margin, made of one cell (or even absent in sterile shoots), while *P. elatum* has teeth regularly with (1)2−3 cells per tooth (also on sterile shoots), and more irregularly arranged areolation of short elongate cells, while the areolation in *P. elatum* is made of regularly elongate, ± rectangular cells often in clear diagonal rows from the costa towards the leaf border. The only morphological reminescences from *P. elatum* are shortly decurrent leaves in fertile shoots of *P. curvatulum*, and even these may be absent from leaves on sterile shoots. *P. elatum* has always rather broad and long-decurrent leaves. The character not present in any other of the related taxa of *Plagiomnium* sect. *Rosulata* is the yellow color of c. ¾ of the seta length in *P. curvatulum*.

Plagiomnium drummondii

Plagiomnum drummondii has a boreal, holarctic range in the boreal bioclimatic vegetation zone (McIntosh & Newmaster, 2014a, Koponen & Ignatova 2018). In Europe, it occurs rarely only in eastern part. It belongs to the section *Plagiomnium* and resembles most *P. japonicum*, both being larger in size and in having larger teeth of leaf margin than three other species of the section, *P. acutum*, *P. floridanum* and *P. cuspidatum*. According to Harris (2008, fig. 4), *P. drummondii* (n = 6) and *P. japonicum* (n = 7) are sister taxa and form a sister group to the other species of the section *Plagiomnium*. On the basis of the chromosome numbers they hardly are a dioicous − monoicous species pair. According to Wyatt & Odrzykoski (1998) "*Plagiomnium japonicum* is most genetically similar to *P. drummondii*, but these species are highly distinctive genetically from all other species".

Plagiomnium novae-zealandiae

There seems not to be any suitable dioicous counterpart to synoicous *Plagiomnim novae-zealandiae***.** It has been given as synonymous with synoicous *P. rostratum*, which differs by non-decurrent leaves versus decurrent leaves in *P. novae-zealandiae.* Koponen (1982a) and Koponen and Sun (2017) hypotetized on the origin of synoicy in *Plagiomnium* sect. *Rostrata*. If it took place only once, in old Gondwanaland, this could explain the presence of synoicous *P. novae-zealandiae* in New Zealand and S Australia. If synoicy was borne only once but in SE Asia, the existence of synoicous *P. novae-zealandiae* is difficult to explain.

Plagiomnium rostratum

Synoicous *Plagiomnium rostratum* has a temperate – southern boreal range in North America and Europe. In Asia, it has some disjunct localities around the Lake Baikal area, in Western Himalaya and in Gansu − Sichuan provinces of China (range map in Koponen 1982a, c; Koponen 2014a). It differs from most other species of *Plagiomnium* section *Rostrata* by having non-decurrent leaves. The other *Plagiomnium* species with non-decurrent leaves are *P. ellipticum* (see above) and *P. succulentum*, but DNA characters show that *P. succulentum* is near the species of the genus *Orthomnion* (Koponen & Sun 2017). Morphologically, the synoicous race of *P. succulentum* does not differ from its dioicous race (see above). The two other common dioicous species of the section *Rostrata* in Asia are *P. integrum* and *P. maximoviczii*. *P. integrum* has smaller but not sympatric range with the range of *P. rostratum*, has decurrent leaves, and larger elongate leaf cells, while the cells in *P. rostratum* are smaller and ± isodiametric. *P. integrum* grows in many kinds of substrates (Koponen 1972a, 2014c, 2017, Koponen & Norris 1983), while *P. rostratum* is a calcicole species. For these facts *P. rostratum* cannot be the synoicoius counterpart of dioicous *P. integrum.*

Plagiomnium maximoviczii has smaller leaf cells than *P. rostratum*, but the other characters such as the juxtacostal cells and the structure of leaf marginal teeth, and DNA characters suggest that it preferably is a pair of synoicous *P. rhynchophorum* (see above). In Harris's (2008, fig 2 and 4) cladograms *P. rostratum* is in the same glade with *P. maximoviczii* and *P. novae-zealandiae*.

Plagiomnium venustum

Plagiomnium venustum is an endemic of the Pacific coastal areas of North America and it has no morphologically similar relatives.

Species with only dioicous plants

The family Mniaceae has 74 species (Koponen 2017), plus *Cinclidium minutifolium* (Koponen & Ignatova 2018) and 69 of them are dioicous and four species are either dioicous or monoicous. The dioicous taxa, discussed with their monoicous pairs above are also included in the list below.

The dioicous taxa are grouped according to their distribution areas into phytogeographic groups or floristic elements. The phytogeographic code is that used in "Index Muscorum". The parenthesis indicate areas from which I have not seen correctly identified specimens.

Continuously or disjunctively ranging holarctic taxa

Cinclidium Sw.
- *arcticum* (Bruch & Schimp.) Schimp. – Am1 As1 (As2) Eur
- *latifolium* Lindb. – Am1 As1 Eur
- *minutifolium* Broth. – (Am 1) As 1 Eur

Cyrtomnium Holmen
hymenophylloides (Hübener) T.J. Kop. – Am1 As1 As2 Eur
hymenophyllum (Bruch & Schimp.) Holmen – Am1 As1 Eur
Mnium Hedw.
lycopodioides Schwägr. – Am1 As1−As5 Eur
blyttii Bruch & Schimp. – Am1 As1 Eur
hornum Hedw. – Afr1 Am1 As5 Eur
spinosum (Voit) Schwägr. – Am1 As1−As3 As5 Eur
stellare Hedw. – Afr1 Am1 As1−As3 As5 Eur
thomsonii Schimp. – (Afr1) Am1 As1−As3 As5 Eur
Plagiomnium T.J. Kop.
ellipticum (Brid.) T.J. Kop. – (Afr1) Am1 Am6 As1−As3 As5 Eur
Pseudobryum (Kindb.) T.J. Kop.
cinclidioides (Hübener) T.J. Kop. – Am1 As1−As3 Eur
Rhizomnium (Broth.) T.J. Kop.
andrewsianum (Steere) T.J. Kop. – Am1 As1 Eur
gracile T.J. Kop. – Am1 As1 (As2) Eur
magnifolium (Horik.) T.J. Kop. – Am1 As1−As3 Eur

Mnium hornum was previously recorded from Japan and its neighbouring areas but it showed to be a different species, *M. orientale* (Wyatt *et al.* 1997). Accordingly, *Mnium hornum* occurs only in western N America and Europe and its neighbouring areas. *M. spinosum* is disjunctively Holarctic (see above). *Plagiomnium ellipticum* is bipolar occurring in S Chile and S. Argentina (Koponen 1971a).

East Asia – NW North America

Rhizomnium (Broth.) T.J. Kop.
nudum (E.G. Britton & R.S. Williams) T.J. Kop. – Am1 As1 As2
Trachycystis Lindb.
flagellaris (Sull. & Lesq.) Lindb. – Am1 As1 As2

A number of bryophytes occurring in SE Asia extend their range along the Aleutians to Alaska and Pacific N America. They are named as North Pacific or Beringian element.

Western North America

Leucolepis Lindb.
acanthoneura (Hook.) W.C. Steere – Am1
Mnium Hedw.
arizonicum J.J. Amann – Am 1
Plagiomnium T.J. Kop.
insigne (Mitt.) T.J. Kop. – Am1
Rhizomnium (Broth.) T.J. Kop.
glabrescens (Kindb.) T.J. Kop. – Am1

Mnium arizonicum differs from the species Pacific Coast element by that its range extends farther east in the inland and to Greenland (Koponen 1972b, McIntosh & Newmaster 2014b).

Eastern North America

Plagiomnium T.J. Kop.
floridanum R. Wyatt & Ordzykoski – Am1
ciliare (Müll.Hal) T.J. Kop. – Am1
Rhizomnium (Broth.) T.J. Kop.
appalachianum T.J. Kop. – Am1
chlorophyllosum (Kindb.) T.J. Kop. – Am1

Plagiomnium ciliare, *Rhizomnium applachianum* and *R. chlorophyllosum* have rather wide ranges in coastal N America, the Appalachians and S Canada (Koponen 1971a, 1973a). As to *Plagiomnium floridanum*, see above. *Rhizomnium chlorophyllosum* was previously united collectively to the European *R. punctatum* (see Koponen & Sun 2017).

Europe

Plagiomnium T.J. Kop.
- *affine* (Funck) T.J. Kop. – Afr1 As5 Eur
- *elatum* (Bruch & Schimp.) T.J. Kop. – (Afr1 As5) Eur
- *undulatum* (Hedw.) T.J. Kop.
  - var. *undulatum* – Afr1 Afr2 (Am1 Am6, introduced) As5 Eur
  - var. *madeirense* T.J. Kop & Sergio − Afr1 Eur

Rhizomnium (Broth.) T.J. Kop.
- *punctatum* (Hedw.) T.J. Kop.
  - var. *punctatum* – Afr1 As1 As5 Eur
  - var. *hermanperssonii* T.J. Kop. – Eur

The species of the European group are either restricted to Europe (*Plagiomnium elatum*) or occur also in Europe and neighbouring N Africa and Minor Asia (*P. affine*, *P. undulatum*, Koponen 1971a, 1993). *R. punctatum* has disjunct localities in Central Siberia (Koponen & Afonina 1993). In this connection it may be noted that in North America not a single species of *Plagiomnium* section *Undulata* occurs, except the introduced populations.

Temperate to meridional SE Asia

Mnium Hedw.
- *orientale* R. Wyatt, Ordzykoski & T.J. Kop. – As2
- *heterophyllum* (Hook.) Schwägr. – As1−As3 As5 Eur

Orthomnion Wills.
- *bryoides* (Griffith) Nork. – As2 As3
- *handelii* (Broth.) T.J. Kop. – As2
- *javense* (M. Fleisch.) T.J. Kop. – As2−As4
- *noguchii* T.J. Kop. – As3
- *nudum* E.B. Bartram – As2 As3
- *piliferum* T.J. Kop. – As2
- *yunnanense* T.J. Kop., X.J. Li & M. Zang – As2 As3

Plagiomnium T.J. Kop.
- *acutum* (Lindb.) T.J. Kop. – As1−As3
- *arbuscula* (Müll.Hal.) T.J. Kop. – As2 As3
- *confertidens* (Lindb. & Arn.) T.J. Kop. – As1 As2 (As5) Eur
- *guizhouense* Y.J. Jia & S. He – As2
- *japonicum* (Lindb.) T.J. Kop. – As1−As3
- *maximoviczii* (Müll.Hal.) T.J. Kop. – As2 As3
- *tezukae* (Sakurai) T.J. Kop. – As 2
- *vesicatum* (Besch.) T.J. Kop. – As1 As2

Pseudobryum (Kindb.) T.J. Kop.
- *speciosum* (Mitt.) T.J. Kop. – As2

Rhizomnium (Broth.) T.J. Kop.
- *hattorii* T.J. Kop. – As2
- *horikawae* (Nog.) T.J. Kop. – As2 As3
- *striatulum* (Mitt.) T.J. Kop. – As1−As3
- *tuomikoskii* T.J. Kop. – As1 As2
- *parvulum* (Mitt.) T.J. Kop. – As1−As3

Trachycystis Lindb.
- *microphylla* (Dozy & Molk.) Lindb. – As1 As2
- *ussuriensis* (Maack & Regel) T.J. Kop. – As1−As3 As5

The Mniaceae is richest in species in temperate to meridional SE Asia. Most of the species belong to Himalayan−Japanese element ranging from Japan to the Himalayas. This element can be divided into several subelements (e.g. Koponen 2014a). A number of species range from the Himalayas to central China (*Plagiomnium arbuscula, P. yunnanense*, see below). Some of the taxa are endemics in limited areas, *Pseudobryum speciosum* in Japan, *Orthomnion handelii* in the Sino-Himalayas and *Plagiomnium quizhouense* in Quizhou Province in China. *Mnium orientale* (Koponen & Ignatova 2018) and *Plagiomnium vesicatum* (Koponen 1972a, 2014a) occur in Japan and neighboring Korea and Russian Far East. *Rhizomnium horikawae* has the range disjunct between Taiwan and the Himalayas, similar to that of synoicous race of *R. magnifolium*.

Two of the species, *Mnium heterophyllum* and *Trachycystis ussurienssis* show old connection from SE Asia to Europe by ranging via the Himalayas to Caucasus area. Still more convincing of the earlier wider ranges are *Trachycystis microphylla* and *T. flagellaris*. They are known from Baltic amber born c. 44 million years ago (Frahm 2010). *Plagiomnium confertidens* has a rather northern range in Asia (Koponen & Ignatova 2018) and could be included in the group of "Continuously or disjunctively ranging holarctic taxa" as well.

Meridional to (sub)tropical SE Asia

Orthomnion Wills.
elimbatum (Nog.) T.J. Kop. – As 4 Austr1
Plagiomnium T.J. Kop.
cordatum T.J. Kop. & D.H. Norris – As4
elimbatum (M. Fleisch.) T.J. Kop. – As4
integrum (Bosch & Sande Lac.) T.J. Kop. – As2−As4 Oc
succulentum (Mitt.) T.J. Kop. – As2−As4

Of these taxa, *Plagiomnium integrum* and *P. succulentim* extend their ranges from continental SE Asia to New Guinea (Koponen 2017). *Plagiomnium cordatum* is a New Guinean endemic, and *Orthomnion elimbatum* nearly so (Koponen & Norris 1983). *Plagiomnium elimbtum* has an area from Java to continental Malaysia.

Summary and conclusions

Prerequisities of species pairs

1) One of the pairs is dioicous and the other is monoicous, and usually synoicous.
2) The chromosome number of the monoicous plant is double compared with dioicous plant.
3) The gametophytes of the monoicous plant are larger.
4) The leaf cells of the monoicous plant are larger.
5) The ranges of monoicous counterparts are in most cases wider than the ranges of dioicous counterpart and the ranges are sympatric. Most of them have similar habitat ecology.

Characters observed not being affected by doubling of the chromosomes

Leaf shape, leaf cell shape, structure of leaf marginal teeth, costa and leaf decurrency are similar in autopolyploid species pairs.

Identification and taxonomic level

The fertile plants of species pairs can always be separated by difference in the sexual condition. Moreover, perigonia of dioicous species differ from perichaetia of monoicous species, perigonial leaves having a different shape than perichaetial leaves. Even the non-fertile plants can be identified on the basis of the size of the plants and laminal cells, but not in all cases (Chapter 2.2.). Should these cryptic monoicous plants be separated at the specific or some other taxonomic level from the dioicous plants remains an open question (see below).

Addition to the nomenclature

Jia and He (2015) transferred *Orthomnion wui* to *Plagiomnium* as *P. wui* (T.J. Kop.) Y.J. Jia & S. He. Although its sporophyte has not been found, their decision was well founded. As discussed above, synoicous *O. wui* cannot be morphologically distinguished from dioicous *Orthomnion yunnanense*. I have seen a fruiting specimen of *O. yunnanense* (China. Yunnan, Gaolingshan region, 2015 *J.R. Shevock 46507, W. Ma & Y. Yao*, in H). The capsule is similar to the capsules in *Plagiomnium* and the peristomes are complete. Thus, the combination of *O. yunnanense* to *Plagiomnium* is well founded. If the proposal by Ochyra *et al.* (2017) to conserve *Plagiomnium* against *Orthomnion* and *Orthomniopsis* is accepted, the other species of *Orthomnion* will suffer the same destiny as well.

Plagiomnium yunnanense (T.J. Kop., X.J. Li & M. Zang) T.J. Kop., **comb. nov.**

Basionym: *Orthomnion yunnanense* T.J. Kop., X.J. Li & M. Zang, Ann. Bot. Fennici 19: 73. 1982.

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